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MATURATION OF THE NIGHT SHARK, *CARCHARHINUS SIGNATUS*, IN THE SOUTHWESTERN EQUATORIAL ATLANTIC OCEAN

Fabio H. V. Hazin, Flavia M. Lucena, Tatiane S. A. L. Souza, Clara E. Boeckman, Matt K. Broadhurst and Roberto C. Menni

ABSTRACT

Over 700 night sharks, *Carcharhinus signatus*, comprising 327 females and 417 males were collected from semi-pelagic longliners operating throughout the south-western equatorial Atlantic between October 1992 and May 1997. Analysis of various morphometric relationships showed significant differences between males and females for regressions of precaudal length (PL) and interdorsal space (IS) and for total weight (TW) and evicerated weight (EW) and headless finned and evicerated weight (HW). A common log EW/log TL regression was calculated for both sexes: log EW = −12.03 + 2.93 log TL. Females and males were categorized into maturation stages (5 and 3, respectively) according to morphological changes in their gonads. The majority of specimens were sexually immature. The size at sexual maturity for females was estimated at between 200 and 205 cm TL, while males matured at between 185 and 190 cm TL. A seasonal peak in male GSI during spring, combined with evidence of female ovulation shortly after suggests that copulation occurs in summer. Gravid females had between four and 15 pups varying in total length from 10 to 40 cm.

The night shark, *Carcharhinus signatus*, is an oceanic species commonly inhabiting outer continental shelf areas in depths generally exceeding 100 m (Bigelow and Schroeder, 1948; Springer, 1963; Branstetter, 1981; Menni et al., 1995; Hazin et al., 1998). Originally described as *Hypoprion signatus* and *H. bigelowi* (Poey, 1868; Cadenat, 1956; Raschi et al., 1982), its main distribution and abundance appears to be in the Atlantic Ocean, extending from Argentina and southern Brazil (Krefft, 1968; Garrick, 1985; Menni et al. 1995; Chiaramonte, 1998) to Delaware, U.S.A. (Compagno, 1984) and along the west coast of Africa (Cadenat, 1956). There have also been some unconfirmed reports of individuals captured off the west coast of Panama (Compagno, 1984).

Night sharks typically have been retained as a commercial by-catch from semi-pelagic longline fisheries targeting billfishes and tunas (Branstetter, 1981; Hazin et al., 1998). However, in recent years off the northeast coast of Brazil, due to increases in the value of their meat and fins and the discovery of localized areas of relatively large abundances (i.e., around seamounts), there has been a trend towards direct targeting (Menni et al., 1995; Hazin et al., 1998). Despite their commercial importance, apart from some early taxonomic work (e.g., Poey, 1868; Bigelow and Schroeder, 1948; Cadenat, 1956; Raschi et al., 1982) there is very little information available, particularly with respect to important life history traits such as reproductive biology. Of the few studies done in this area, most have been limited by small sample sizes and only include brief descriptions of the reproductive anatomy and maturation stages of individual females (e.g., Bigelow and Schroeder, 1948; Raschi et al., 1982; Bransetter, 1981).

Because most carcharhinids are characterized by low rates of population increase, adequate knowledge of the life history of night sharks is essential to ensure their sustainable exploitation off north-eastern Brazil. Our main aim in the present study, therefore, was to

provide a first step in addressing this absence of information, via an examination of their maturation. In addition, because often only dressed or partially dressed carcasses are landed at Brazilian ports, we aimed to provide some supplementary information on morphology, so that for future fishery-dependent studies, proportions of landed carcasses can be indexed against total length (TL) and weight.

Methods

This study was based on 744 specimens collected from the catches of four Brazilian longliners operating in the south-western equatorial Atlantic Ocean (Fig. 1) between October 1992 and May 1997. The configurations of longlines used among the different vessels remained similar over the period examined (see Hazin et al., 1998 for details) and basically consisted of multifilament mainlines with secondary lines attached in clusters of six to seven, separated by styrofoam buoys. The types of hooks varied among three main brands (depending on availability) however, relative sizes remained the same throughout the period examined. Fishing methods and operations were similar across vessels, with the mainline-set beginning at about 02:00 and ending at dawn. The gear was then left to fish for about 6 h, before retrieval began at noon and ended at dusk. The primary bait

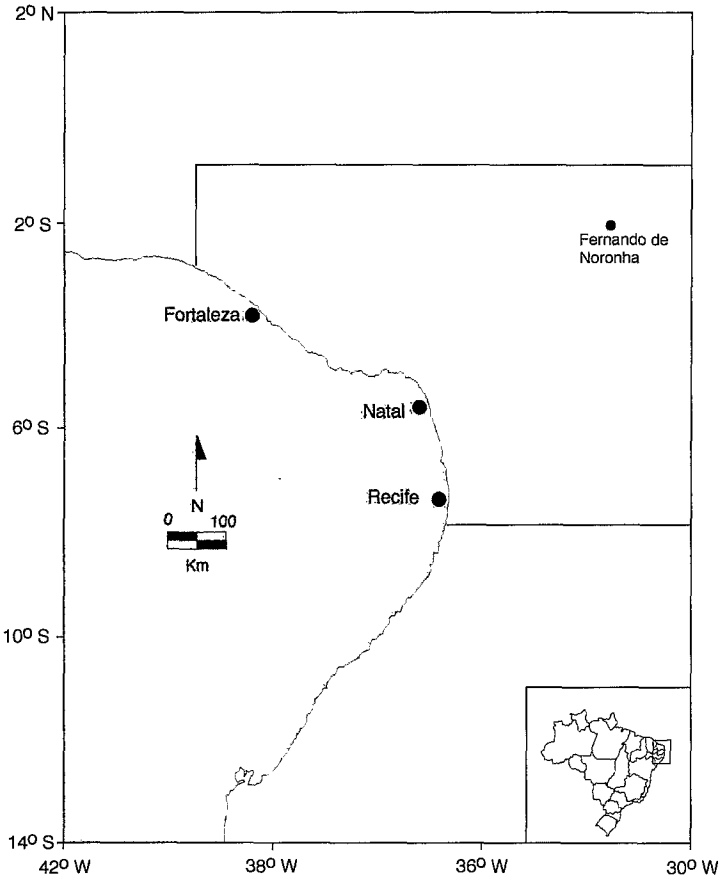

Figure 1. Location of fishing area.

was the Brazilian sardine, *Sardinella brasiliensis*, although some other species, including flying fish, *Cypselurus cyanopterus*, and squid, *Loligo* sp., were occasionally used.

DATA COLLECTED.—Sharks were measured, weighed and dissected as soon as possible after being captured. To firstly provide some information on morphology (for indexing various body measures against total length), data on TL (measured as per the methods described by Garrick, 1982), precaudal length (PL), fork length (FL), interdorsal space (IS), total weight (TW), eviscerated weight (EW) and headless, finned and eviscerated weight (HW) were recorded from a sub-sample of males and females. Data collected from all other specimens included, date of capture, sex, total length and eviscerated weight. Data collected from females included, diameter of the largest ovarian follicle, weight and width of the oviducal gland and functional ovary, width of uteri and the presence of eggs or embryos. The length, width and weight of testes, width of epididymis, length and calcification stage of claspers and the presence of seminal fluid in ampulla ductus deferens were recorded from males. Reproductive organs were measured to the nearest 0.1 mm using vernier calipers.

Female maturation stages were mainly evaluated according to changes in the diameter of the largest ovarian follicle and to a lesser extent, the weight and width of the oviducal gland. Five stages were proposed including, juvenile, maturing, pre-ovulatory, ovulating and gravid (see results for details of each stage). Males were divided into three stages of maturation (juvenile, maturing and adult) according to gonad development and in particular, the size and calcification of claspers combined with changes in epididymides and ampullae

ductus deferens. A gonosomatic index (GSI) for mature males was calculated by dividing weight of testes by eviscerated weight × 1000. Insufficient data precluded the analysis of GSI per month and data were pooled across seasons throughout the year.

STATISTICAL ANALYSIS.—Linear regressions of various morphological relationships were calculated separately for males and females, tested for heteroscedasticity using the variance ratio test then analyzed using analysis of co-variance (ANCOVA). Appropriate combined or pooled regressions were calculated for relationships that showed no significant differences between sexes. Data describing seasonal changes in diameter of the largest ovarian follicle for females and GSI for mature males were tested for heteroscedasticity using the Scheffé-Box test, transformed if necessary and then analyzed separately using one-factor analysis of variance. Significant differences between means were separated using Scheffé's multiple comparison of means test. Size-frequency distributions of males and females were compared using two-sample Kolmogorov-Smirnov tests ($P = 0.05$). A chi-square goodness of fit test was used to examine the hypothesis of an equal sex ratio among pups from gravid females.

RESULTS

MORPHOLOGICAL CHARACTERISTICS.—Two-sample Kolmogorov-Smirnov tests showed no significant differences in the size-frequency compositions between males (417) and females (327) used in the study (Fig. 2). ANCOVA detected significant differences between males and females in elevation for the regression of PL and IS and in regression coefficients for TW versus EW and HW (Table 1). There were no other significant differences detected between males and females for the relationships examined (Table 1). A common log EW/log TL regression was calculated (Table 1).

STAGES OF FEMALE MATURATION.—Most specimens were considered juveniles (65% of total caught) ranging in size from 110 to 192 cm TL with filiform uteri and oviducal glands only slightly delineated (Fig. 3B, Table 2). Their ovarian follicles were translucent and small in diameter (Fig. 3A, Table 2), while ovaries were light, undeveloped and, in the majority of cases, not fully differentiated from the epigonal organ. Uterus width ranged from 0.1 cm to 4.5 cm (Table 2). Specimens classified in the maturing stage ranged from 159 to 194 cm TL, had enlarged oviducal glands that were clearly discernible (e.g., from

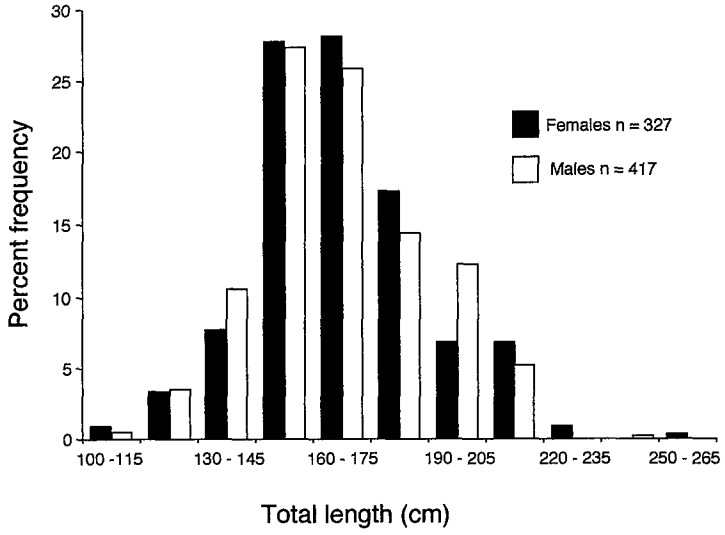

Figure 2. Length-frequency distributions of male and female night sharks used in the study.

1–3.5 cm in width, Fig. 3B, Table 2). Their functional ovary had increased in size and weight and was differentiated from the epigonal organ. Ovarian follicles were white and opaque and had begun to increase in diameter (e.g., 0.5–1.5 cm, Fig. 3A, Table 2). Uterus width was not greatly different from individuals in the juvenile stage (Table 2). Pre-ovulatory specimens ranged in size from 175.5 to 221.5 cm TL and most had enlarged uteri and oviducal glands (Fig. 3B, Table 2) with evidence of vitellogenesis. Most ovarian follicles were yellow and the majority had a diameter greater than 1 cm (Fig. 3A, Table 2). Although some ovulating females (210 to 252 cm TL) had eggs in their uteri, and therefore might be classed as gravid, these were differentiated (from gravid females) on the basis of having fully developed vitellogenic follicles in their ovaries, enlarged oviducal glands (Fig. 3B, Table 2) and follicles present in the oviduct. In comparison to these individuals, gravid females (210 to 252 cm TL), had much lighter and narrower ovaries with many corpora lutea present. They also showed greater variability in width of their uteri (Table 2). Four of the 16 ovulating and pregnant females showed evidence of mating scars.

The relative abundance of females in different stages of maturation showed that juveniles, maturing and pre-ovulating individuals were present in catches throughout the year (Fig. 4A). Gravid females were mostly caught during summer with a decreasing trend in relative catches through to winter, while ovulating females were recorded only during summer (Fig. 4A). ANOVA detected significant differences in seasonal variation of the diameter of the largest ovarian follicle (data were treated in the raw form; $F = 7.816$; $P = 0.003$). Scheffé's multiple comparison of means test showed that mean diameter was significantly larger in summer than the rest of the year (Fig. 4B, $P < 0.05$).

The uterine contents of the nine gravid females captured during the study are summarized in Table 3. All embryos from individual gravid females showed a similar stage of development. They were longitudinally orientated (in the same direction as the mother) in individual chambers with a long yolk stalk and yolk-sac placenta connected to the uterine wall. Their bodies were uniform brownish-gray with a black tip on the anterior portion of

Table 1. Summaries of linear regressions for male and female night sharks, F ratios from ANCOVA testing regression coefficients (β) and elevations (α) and where apropriate, common regressions. TL = total length; PL = precaudal length; FL = fork length; IS = interdorsal space; TW = total weight; EW = eviserated weight; HW = headless, finned and eviserated weight; r^2 = coefficient of determination; n = number of specimens; **significant at P < 0.01; 3 = common population regression coefficients (i.e., –2.14 and –0.92).

Males			Females			F ratios		
Regression	r^2	n	Regression	r^2	n	β	α	Common regression
FL = 4.31 + 0.79TL	0.97	46	FL = 6.26 + 0.78TL	0.98	47	0.12	0.38	FL = 5.66 + 0.78TL
PL = -3.04 + 0.76TL	0.98	64	PL = –3.74 + 0.76TL	0.99	59	0.15	1.48	PL = –3.33 + 0.77TL
IS = -3.21 + 0.26TL	0.92	66	IS = –3.46 + 0.26TL	0.93	61	0.01	3.23	IS = –3.46 + 0.26TL
PL = -7.87 + 0.97FL	0.98	44	PL = –7.18 + 0.97FL	0.98	45	0.01	0.36	PL = –7.29 + 0.97FL
IS = -1.57 + 0.31FL	0.90	46	IS = –4.18 + 0.32FL	0.91	47	0.36	2.10	IS = –3.39 + 0.32FL
IS = -2.14 + 0.34PL	0.91	77	IS = –0.92 + 0.32PL	0.97	64	0.99	11.63**	IS = 3 + 0.33FL
EW = 1.27 + 0.83TW	0.97	63	EW = 2.72 + 0.76TW	0.97	54	12.66**		
HW = 0.03 + 0.68TW	0.98	61	HW = 2.96 + 0.58TW	0.78	44	7.72**		
logEW = -12.10 + 2.95 logTL	0.93	393	logEW = –11.93 + 2.92 logTL	0.94	287	0.28	0.22	logEW = –12.03 + 2.93 logTL

Table 2. Characteristics of female night sharks in each maturation stage and the length range and number of specimens.. All lengths are in cm and weights in g; Dia. = diameter.

Characteristic	Juvenile	Maturing	Pre-ovulatory	Ovulating	Gravid
Dia. of largest ovarian follicle	< 0.5	0.5–1.5	0.9–2.9	2.8–4.6	< 0.8
Width of oviducal gland	< 1.0	1.0–3.5	2.3–3.9	2.8–5.9	3.2–4.0
Weight of oviducal gland	< 1.0	1.0–10.0	4.0–24.0	12.5–37.2	10.1–15.0
Width of ovary	0.3–6	1.5–5.5	3.0–8.5	5.5–8.8	4.8–6.5
Weight of ovary	2.0–34	5.0–67.7	11.5–159.5	98.0–247.1	17.0–121.5
Width of uteri	0.1–4.5	0.2–4.5	1.9–9.2	5.5–11.2	1.5–18
Total length of specimens	110.0–192.0	159.0–194.0	175.5–221.5	210.0–252.0	210.0–252.0
Number of specimens	212	60	39	7	9.

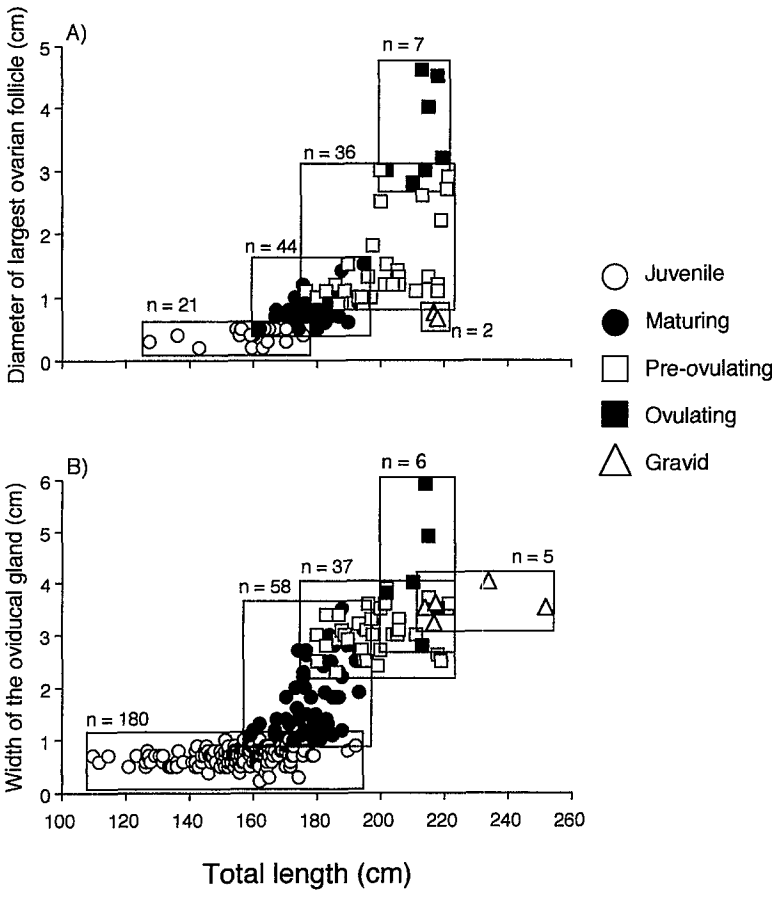

Figure 3. Relationships between total length and: A) diameter of largest ovarian follicle and B) width of oviducal gland across the various stages of maturation.

their caudal fins. Sex ratios of embryos in individual gravid females varied considerably, but the total pooled ratio was not significantly different from 1:1 ($\chi^2 = 2.56$, P = 0.11).

STAGES OF MALE MATURATION.—Most specimens were juveniles (63%) ranging in size from 110 to 180 cm TL (Fig. 5). These individuals had thin epididymides and filiform ampulla ductus deferens without seminal fluid. Claspers were flexible, varying in length from 3.5 to 21 cm (Fig. 5), while testes were small, light and not fully differentiated from the epigonal organ. Maturing individuals ranged in size from 160 to 190 cm TL and had claspers that were beginning to calcify and enlarge (Fig. 5). Their epididymides showed evidence of thickening and in some individuals, seminal fluid was found in the ampullae ductus deferens. All males greater than 190 cm TL had completely developed sexual organs, including fully calcified and rigid claspers (15 to 26 cm in length, Fig. 5), thick epididymides and circumvoluted ampullae ductus deferens. The weights of their testes varied from 5 to 175 g.

ANOVA detected significant differences in seasonal variation of GSI for mature males (data were ln(x+1) transformed; F = 49.3, P = 0.0001). Scheffé's multiple comparison of

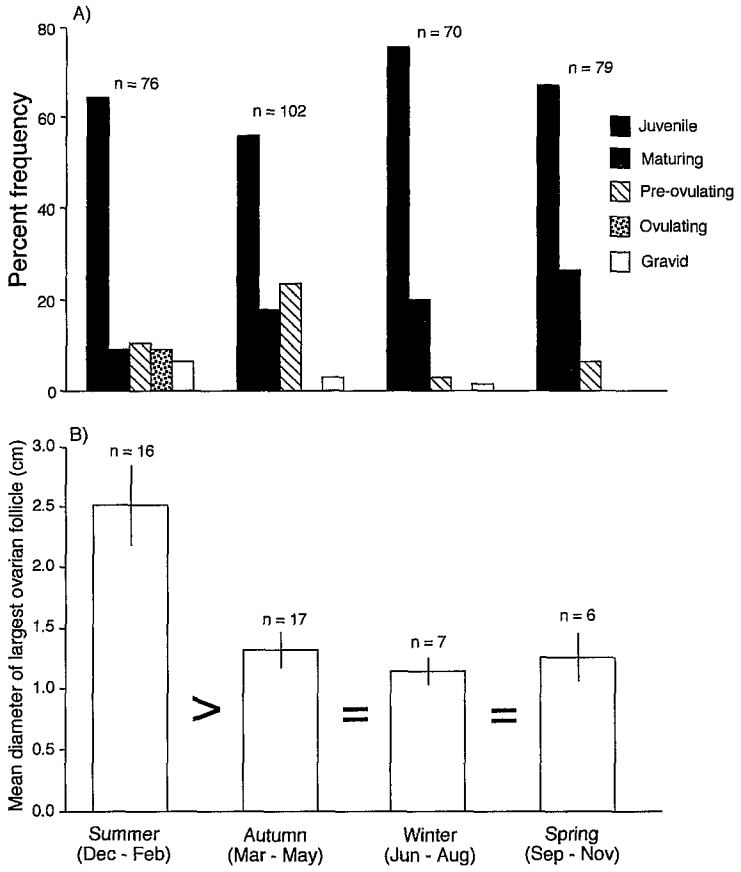

Figure 4. A) seasonal relative abundance of females in catches according to their stage of maturation and B) differences in mean diameter of largest ovarian follicle (± SE) in mature females between seasons. > and = indicate direction of differences detected in Scheffé's multiple comparison of means test.

Table 3. Summaries of the month of capture, total length (TL), number and sex of embryos found in the nine gravid night sharks. TL in cm.

Month of capture	TL of gravid specimen	TL range of embryos	Number of embryos	
			Male	Female
February	210	11.7–14.2	7	8
February	218	10.0–13.0	1	12
February	210	17.0–21.0	6	4
February	204	35.0–40.0	2	2
February	234	12.0–14.8	8	5
March	217	14.8–23.0	6	9
May	214	26.0–29.5	5	5
May	252	32.5–35.0	1	8
June	217	31.8–37.2	6	5

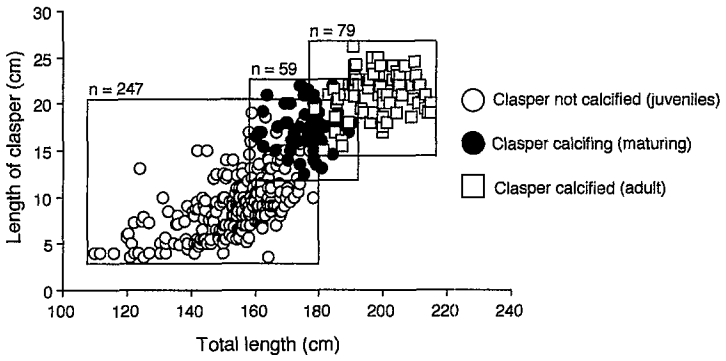

Figure 5. Relationship between total length and length of claspers for males across stages of maturation.

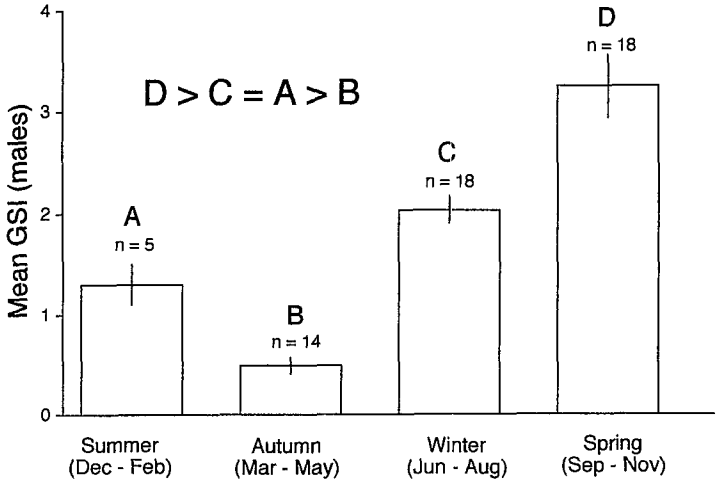

Figure 6. Differences in mean GSI (± SE) of mature males between seasons. > and = indicate direction of differences detected in Scheffé's multiple comparison of means test.

means test showed that compared to all other seasons, mean GSI was significantly greater in spring and lowest in autumn (Fig. 6, $P < 0.05$).

Discussion

Morphometric analysis of some specimens showed that body measurements such as PL, IS and FL can be used as reliable estimators of TL across both sexes. While a common regression can be used to index EW against TL (Table 1), it is apparent that the relationships between TW, EW and HW were significantly different between sexes, probably due to temporal and/or gender variability in the weights of gonads. The information obtained from these analyses is important for fishery-dependent studies, since it facilitates the monitoring of size compositions based on various proportions of landed carcasses. Further, while there have been no other studies examining these relationships for

night sharks, the calculated regressions can be applied in future work to examine intraspecific variability among morphometric characteristics from potentially divergent stocks (Garrick, 1982).

Evaluation of the maturation stages of night sharks showed that their reproductive anatomy is very similar to other carcharhinids (Wourms, 1977; Pratt, 1979). Males possess claspers without spurs and have two equally developed testes. Females posses only one functional ovary (right side) composed of many follicles contained in a layer of connective tissue, while oviducal glands are similar in size to those from the blue shark, *Prionace glauca* (Pratt, 1979).

As with many other carcharhinids, the process of maturation in females is closely aligned with development of the oviducal gland (Pratt, 1979). In the present study, this organ increased in width from less than 1 cm in juveniles to 3.5 cm in some maturing specimens (around 175 to 194 cm TL, Fig. 3B). Vitellogenesis only commenced after the oviducal gland had reached 0.9 cm in width. Changes in the diameter of the largest ovarian follicle also facilitated clear delineation among stages of maturation and particularily between pre-ovulating, ovulating and gravid females (Table 2). For example, follicles increased in diameter from a maximum of 2.9 cm in the pre-ovulating stage, to over 4.5 cm in ovulating specimens and then declined to less than 0.8 cm in the two gravid females examined (Fig. 3A).

Compared to the oviducal gland and ovarian follicles, the development of the ovary and uteri showed greater variability (Table 2). The observed differences in changes to the width and weight of the ovary, relative to TL, may be explained by the development of vitellogenic follicles. Because ovary weight is directly determined by the number and size of follicles, they tended to become heavier as follicles developed throughout the first four stages of maturation and were then mostly lighter in gravid females. In contrast, because developing follicles have less influence on the shape of the ovary, the width of ovaries varied considerably, particularly among individuals in the juvenile and maturing stages. Uteri showed little evidence of change between juvenile and maturing females, although in preparation to receive embryos, began to thicken slightly in the pre-ovulating and ovualting stages. Gravid females showed large variability in uteri width, probably owing to their different stages of pregnancy.

Changes to the reproductive organs examined above indicated that females in the present study attained sexual maturity around 200–205 cm TL. Previous studies that have involved examinations of individual specimens close to this size range, but from different areas, provided data that collaborate this estimate. For example, although stage of maturation was not specified, Branstetter (1981) examined a 190 cm TL specimen captured in the Gulf of Mexico and concluded that it was sexually immature, while Raschi et al. (1982), described a 220 cm TL gravid female (with 10 pups) caught off the east coast of Florida.

While it is evident that all females larger than 205 cm TL examined in the present study were sexually mature, the size range at maturity was nevertheless derived using a relatively small sample of ovulating and gravid specimens. Their comparatively low numbers in catches may be explained by at least two hypotheses, including: (1) they were present across the sampled area, but didn't encounter the fishing gear owing to their vertical or temporal distribution and/or feeding behavior or, (2) their abundances were relatively low throughout the fishing area. Given that males were captured in large numbers across all sizes (e.g., 110–220 cm TL, Fig. 2) it is probable that the selectivity of the longlines

encompassed the size range of the large ovulating and gravid females encountered. It is possible, however, that vertical and/or temporal distribution of the longline in relation to their areas and timings of maximum abundance had some effect on selectivity. A related hypothesis is that these females stopped feeding during ovulation and pregnancy (Springer, 1967) and although present, were not sampled by the gear.

Alternatively, copulation, ovulation and pregnancy may occur in other areas. In partial support of this latter hypothesis, there was no evidence to suggest that parturition occurred in the study area. For example, previous studies have shown that individual gravid females can contain pups with lengths greater than 63 cm TL (Bransetter, 1981; Raschi et al., 1982). Based on these studies, Compagno (1984) proposed a size at birth of about 60 cm TL which is substantially larger (e.g., 20 cm) than any of the embryos recorded from gravid females in the present study.

Dermal punctures and lacerations are often inflicted during copulation in carcharhinids and the presence of tooth cuts have been used by several authors to provide evidence of mating (Suda, 1953; Stevens, 1974; Pratt, 1979). In the present study, only four of the ovulating and gravid females examined (16 in total) had relatively new mating scars, suggesting that compared to species such as the blue shark, this is not a common courtship behavior (Hazin et al., 1994). Alternatively, it is also possible that if copulation occurred in different areas (see above) sufficient time may have elapsed for any minor tooth cuts on ovulating and gravid females to heal.

In contrast to female maturation, males showed much clearer, defined stages and approached maturity at smaller sizes. Compared to juveniles, maturing males between 160 and 190 cm TL were characterized by a relatively rapid increase in clasper size and stage of calcification (Fig. 5). Many individuals longer than 180 cm TL and all those larger than 190 cm TL had calcified claspers, indicating that sexual maturity was attained within this size range. A gradual increase in length of their testes provides evidence to support this estimate, although weight varied considerably, with many adult specimens showing light testes. This latter observation may be due to a seasonal cycle of spermatogenesis since GSI for mature males was significantly greatest in spring and lowest in autumn (Fig. 6).

The small sample of mature females makes it is difficult to estimate time of copulation. However, previous studies have shown that the highest mature male GSI typically occurs a few months before mating (owing to the period needed to transfer spermatozoa from the testes to the ampulla ductus deferens) (Teshima, 1981). A significant increase in mature male GSI during spring (Fig. 6), therefore, combined with a greater relative number of gravid females during summer (particularly in February, Table 3) suggests a copulation period throughout summer. The relatively small size of most embryos (mainly 10–20 cm TL) in gravid females caught during February along with some evidence of a general increase in embryo size from February to June (Table 3), supports this estimate.

In addition to providing an overview of maturation, the results from this study have shown that the current exploitation of night sharks off northern Brazil mainly involves juveniles and that like most other elasmobranchs, this species appears to be characterized by a low rate of population increase that may render it susceptible to over fishing. Further research into relevant life history parameters and particularly growth and gestation pe-

riod, as well as abundance, distribution and spatial segregation of mature females is required to facilitate population assessments.

Acknowledgments

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ADDRESSES: (F.H.V.H., F.M.L., T.S.A.L.S., C.E.B., M.K.B) *Universidade Federal Rural de Pernambuco-UFRPE, Departamento de Pesca, Laboratório de Oceanografia Pesqueira, Av. Dom Manuel de Medeiros, s/n, Dois Irmãos, Recife-PE, Brazil, CEP: 52.171-900. Ph/Fax: (081) 441 7276;* (R.C.M.) *CONICET y Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina.*

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